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Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late spring

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Singing by males is a major feature of the mating system of humpback whales, *Megaptera novaeangliae* (Borowski). Although a few songs have been opportunistically recorded on the whales' high-latitude feeding grounds, singing in these regions was thought to be only sporadic. We report results from the first continuous acoustic monitoring of a humpback whale feeding ground (off Cape Cod, MA, USA) in spring. Using autonomous sea-floor recording systems, we found singing on a daily basis over the entire 25 day monitoring period, from 14 May to 7 June 2000. For much of the period, song was recorded 24 h per day. These results, combined with evidence for aseasonal conceptions in whaling catch data, suggest that the humpback whale breeding season should no longer be considered as confined to lower-latitude regions in winter. Rather, we suggest breeding extends geographically and temporally onto feeding grounds into at least spring and early summer. Singing at these times represents either low-cost opportunistic advertising by (perhaps relatively few) males to court females that failed to conceive during the winter, and/or possibly an intrasexual display.

Keywords: humpback whale; song; mating systems; North Atlantic

1. INTRODUCTION

Male humpback whales (*Megaptera novaeangliae*) sing songs that are noteworthy for their length and complexity (Payne & McVay 1971). These songs represent male acoustic displays that are related (directly or indirectly) to mating. Two major hypotheses have been proposed for the function of song in humpback whales: (i) that it serves primarily to attract females (Winn & Winn 1978; Tyack 1981); and (ii) that it establishes dominance rankings among males (Darling & Bérubé 2001). Song is clearly an important element of the humpback's mating system, which has been described as polygynous/promiscuous with some similarity to a lek (Mobley & Herman 1985; Clapham 1996, 2000).

Humpback whales migrate from summer feeding grounds in temperate or polar waters to winter breeding and calving areas in the tropics (Kellogg 1929). In the North Atlantic Ocean, humpbacks occur on several feeding grounds in a range extending from the eastern seaboard of the United States to the Arctic (Smith *et al.* 1999). Individual whales exhibit strong fidelity to particular summering areas (for example, the Gulf of Maine), and there is little exchange among these regions (Katona & Beard 1990). Despite this structuring (which appears to be maintained over an evolutionary time-scale in some areas; Larsen *et al.* (1996)), whales from all of the feeding grounds migrate in winter to a common breeding area in the West Indies (Katona & Beard 1990). There, the whales mix both spatially and genetically (Palsbøll *et al.* 1997).

Breeding in humpback whales is seasonal. Females come into oestrus during winter, and males exhibit a marked increase in spermatogenesis (Chittleborough 1958, 1965). Aggressive intrasexual competition among males frequently occurs during this season (Tyack & Whitehead 1983; Baker & Herman 1984; Clapham *et al.* 1992), and singing is virtually ubiquitous throughout the species' tropical breeding range.

For many years, it was thought that humpback whale singing was confined to tropical waters, although singing has also been documented with some frequency on migratory routes (Clapham & Mattila 1990; Norris *et al.* 1999; Charif *et al.* 2001). So far, there have been few published records of singing in high-latitude feeding areas. Mattila *et al.* (1987) reported isolated records of song off Cape Cod, MA, USA, primarily in late autumn; they suggested that song was rare in spring and relatively common in autumn, and speculated that singing was triggered by the mixing of 'local' whales with others migrating through to different feeding areas. McSweeney *et al.* (1989) obtained two song recordings in August and September in southeastern Alaska; these were the result of listening for short periods over a total of 155 days over five summers. C. Gabriele and A. Frankel (personal communication in 2004) have regularly monitored for humpbacks in Glacier Bay, Alaska, since 2000 and reported singing in late summer and autumn.

We summarize the results of the first continuous acoustic monitoring in late spring on a humpback whale feeding ground, in the Georges Bank area off Cape Cod, MA, USA. We report singing on a virtually daily basis by humpback whales in this area over a 25 day period between 14 May and 7 June 2000, and discuss the implications of these findings for the function of song in this species.

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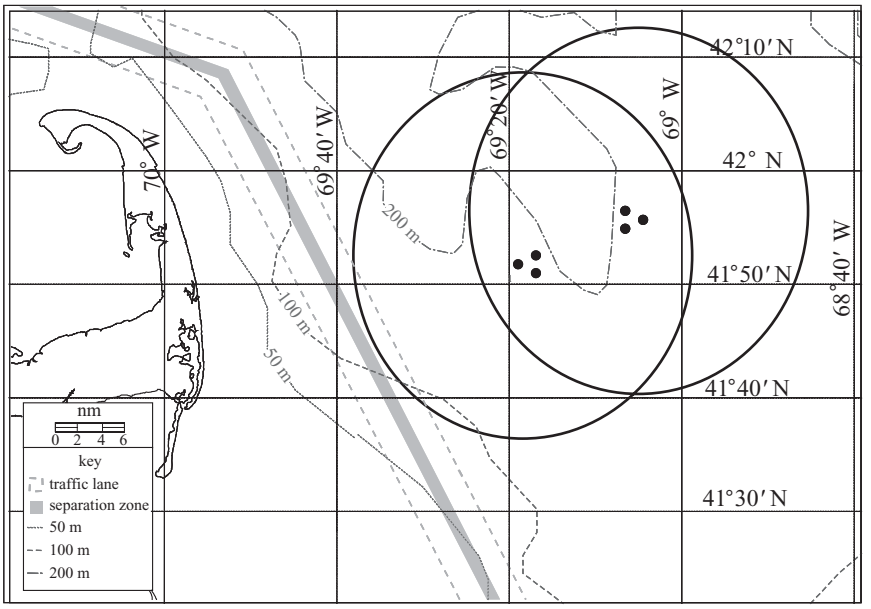

Figure 1. Positions of six pop-up units (black dots) deployed in the western Georges Bank area to the east of Cape Cod, MA, USA. Two arrays of three units each were deployed between 14 May and 7 June 2000. The two large circles delimit potential song detection areas within a radius of *ca*. 29 km.

2. MATERIAL AND METHODS

(a) *Study area*

The western Georges Bank area (WGB; figure 1) is located *ca*. 80–90 nautical miles east of Cape Cod, MA, USA (*ca*. 42° N, 69° W). This area constitutes a moderately shallow (150–200 m depth) bank between Cape Cod to the west, the shallower waters of Georges Bank to the east, and the Great South Channel (GSC) to the south.

Humpback whales from the Gulf of Maine feeding population occupy the WGB and GSC areas from spring to autumn each year. During this time, they forage on small schooling fishes (notably sand lance, *Ammodytes* spp., and herring, *Clupea harengus*) and occasionally on euphausiids (Payne *et al.* 1990). The distribution and abundance of humpbacks in these areas depend upon the location and size of the prey resource; the number of humpback whales observed at any one time in the area has varied from zero to more than 150 (P. J. Clapham, personal observation).

(b) *Acoustic monitoring*

Between 14 May and 7 June 2000, six sea-floor acoustic recorders, referred to as 'pop-ups', were deployed in the WGB at the locations shown in figure 1. Pop-ups were deployed in two triangular arrays of three units per array. Pop-ups within a triangular array were *ca*. 3 km apart, and the centres of the two arrays were 18.4 km apart. A pop-up is an autonomous acoustic recording system consisting of a hydrophone, preamplifier and filter, analogue-to-digital converter, computer, disk drive, batteries and acoustic transponder (Clark *et al.* 2002). For this deployment, the hydrophones (High Tech, Inc. 94-SSQ) and preamplifier systems had a sensitivity of −162 dBV, and were identical. All six units were configured to record continuously at a 2 kHz sampling rate, with an anti-aliasing frequency at 800 Hz. The recording system had a flat frequency response (±1 dB) from 20 to 800 Hz. This frequency band spans the lower frequency range for humpback whale vocalizations, including song.

Based upon detection of one whale at a distance of 29 km (see below), and assuming uniform detection in all directions, the potential monitoring area was estimated at *ca*. 2600 km^2.

(c) *Acoustic analysis*

The primary purpose of the acoustic monitoring was to detect the sounds of North Atlantic right whales (*Eubalaena glacialis*), which are known to occur in the area between about March and July each year. Acoustic analysis of the pop-up data resulted in few detections of right whale sounds, but nearly continuous detections of humpback whale songs. Pop-up data were analysed for humpback singing by using a simple procedure. Recordings from all pop-ups were synchronized (±4 ms) into six-channel data files. Continuous, six-channel spectrograms were scrutinized by analysts familiar with humpback song, using customized software. Each hour of six-channel data (602 h per pop-up; 3612 h total) was scored for the presence or absence of singing, and an estimate was made of the minimum number of whales singing.

Using this analysis, an analyst could not discriminate between three and more than three singers. Consequently, the maximum number of singers counted for any hour was three. Because the occurrence of two or more singers was relatively rare, the data were not confounded by the difficulty of discriminating between multiple singers; however, it is possible that our counts of singers are negatively biased.

To evaluate singing activity level throughout the 25 day recording period, data were summarized in terms of: (i) the daily percentage of hours with at least one singer; and (ii) the daily average number of singers per hour. Diel singing patterns were investigated by summarizing the average number of singers by hour of the day over the 25 day sampling period. Figure 2 is an example of song as recorded on all six pop-ups on 16 May at 00.49 (local time). In a few of the many cases where the same song was recorded on at least three pop-ups, the locations of singers were computed to determine the distance at which singers could be reliably detected (Clark *et al.* 1996; Clark & Ellison 2000).

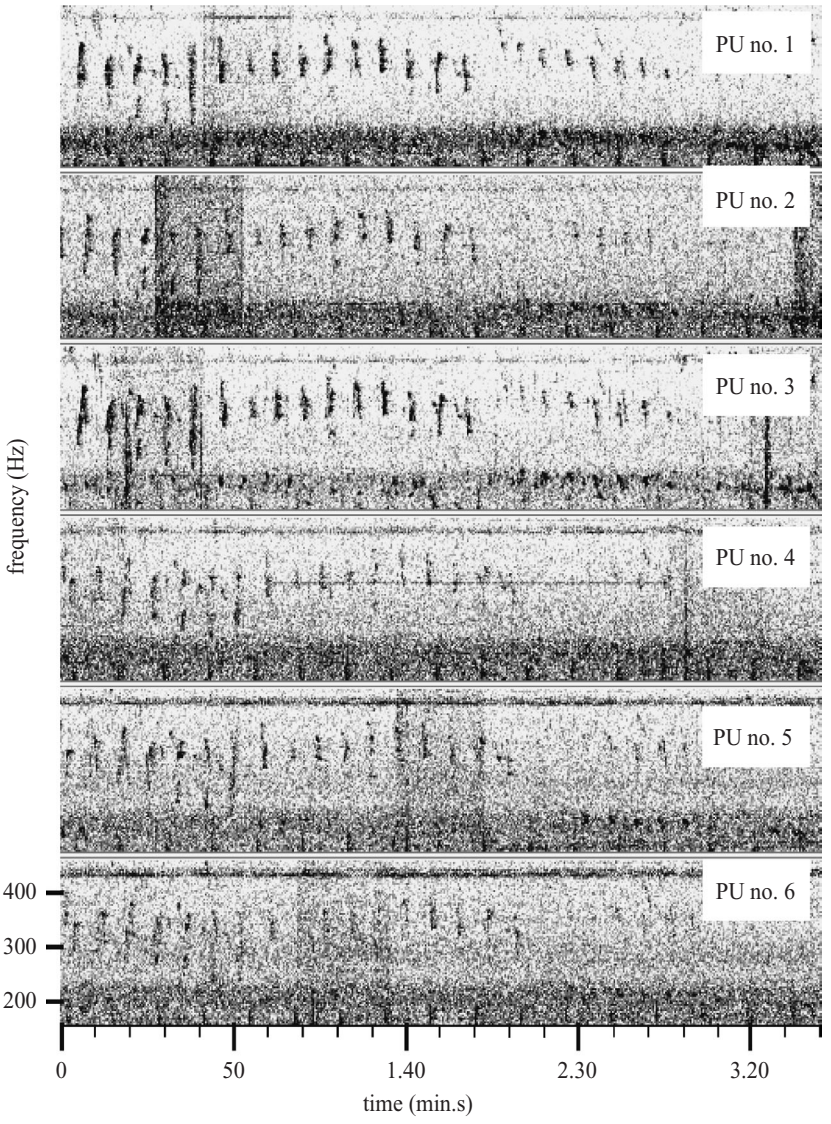

Figure 2. Example six-channel spectrogram showing the same humpback whale song on all six pop-ups (PU). This sample was recorded at 00.49 (local) on 16 May 2000, when the furthest of three singers (shown here) was 29 km from the pop-up 1–2–3 cluster and 18 km from the pop-up 4–5–6 cluster.

3. RESULTS

Humpback whale song data for the period 14 May to 7 June 2000 are summarized in figure 3. From 14 to 30 May 2000 (figure 3*a*), singing was detected during every hour of the day, with the percentage of hours with song decreasing to 58% (14 out of 24 h) by 7 June. This same pattern of decreased singing in late spring was also evident in the average number of singers per hour (figure 3*b*). The highest level of singing occurred on 21 May when there were 12 h with one singer, 11 h with two singers and 1 h with three singers. By 7 June, there were 14 h with one singer and 10 h with no singing. There was no pronounced diurnal pattern in the occurrence of singing (figure 4).

Acoustic locations were calculated for three singers between 22.00 on 15 May and 05.00 on 16 May. Portions of songs for each singer were detectable in the 80–400 Hz band on all six pop-ups. Distances from the three singers' locations to the furthest pop-up were 14, 19 and 29 km, respectively. This equates to a minimum density of 0.0011 singers per square kilometre.

Fortuitously, aerial surveys for monitoring whale populations were conducted by the Northeast Fisheries Science Center during the spring of 2000. These surveys flew over the estimated detection area of the pop-up recorders on 4 days during the acoustic monitoring period. Whales were observed in or on the margin of this area on two days: on 16 May, 25 humpback whales were observed, and on 31 May one humpback was observed. On the other two survey days (15 and 26 May), no humpback whales were observed in the acoustic detection area. Acoustic detections for these four aerial survey days were: minimum of three singers (15 May); minimum of three singers (16 May); minimum of two singers (26 May) and one singer (31 May).

4. DISCUSSION

The results reported here derive from the first effort to continuously monitor humpback whale vocalizations on a feeding ground over an extended period. Our observations demonstrate that, far from being rare or sporadic, singing

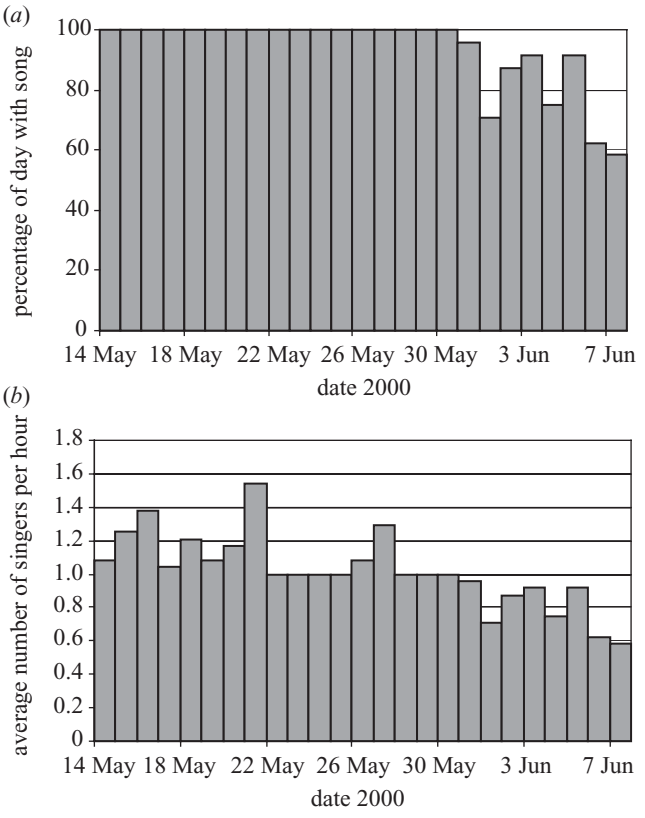

Figure 3. (*a*) The daily percentage of hours with at least one singer. (*b*) The daily average number of singers per hour.

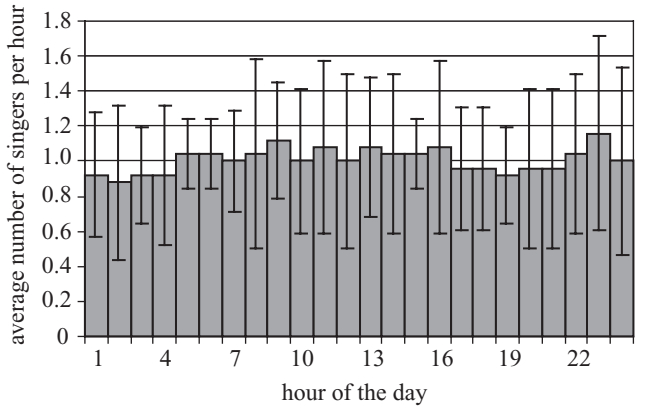

Figure 4. Average number of singers per hour for the 25 day monitoring period.

occurred throughout the day in the study area well into the late spring.

The contrast between these findings and the sporadic records of feeding-ground song reported by Mattila *et al.* (1987) and McSweeney *et al.* (1989) is probably due to major differences in sampling effort because these earlier studies were based upon occasional opportunistic recordings rather than continuous monitoring. Furthermore, our use of pop-ups on the ocean floor greatly extended the range over which humpback whale songs could be detected; the detection range for at least one singer was 29 km, and as noted above the total detection area was *ca*. 2600 km^2. By contrast, both Mattila *et al.* (1987) and McSweeney *et al.* (1989) obtained their recordings using a single hydrophone deployed on a short cable from the surface. This constraint also applies to several published and unpublished records in which humpback whale singing was sought but not heard in the Gulf of Maine or off Alaska (Mattila *et al.* 1987; D. Mattila and P. Clapham, unpublished data; W. Dolphin, unpublished data).

Nonetheless, we cannot exclude the possibility that the continual singing reported here was triggered by specific circumstances that were not present in earlier unsuccessful attempts to detect feeding-ground song. It is unclear whether there is a threshold abundance or density of whales above which singing behaviour is more likely to occur. The 2000 aerial survey data indicated that numerous humpback whales were in the area on at least one of the days on which a minimum of three singers were detected (16 May), but little can be inferred from this because these surveys were not designed to ground-truth the acoustic monitoring. The aerial data probably underestimate the actual number of whales in the area because of detection bias; specifically, some whales may have been underwater when the aircraft passed over, whereas others will have been too far from the trackline for observers to see them. Furthermore, the aerial observations did not cover the entire acoustic detection area on any of these surveys.

The suggestion by Mattila *et al.* (1987) that singing is cued by the mixing of local whales with those from other feeding areas is an unlikely explanation for our results. Photo-identification of individual humpback whales has found little mixing among feeding stocks (Katona & Beard 1990). There are records of Newfoundland humpback whales in the Gulf of Maine in spring or late autumn, but these are few in number and have not occurred in June.

Irrespective of whether humpbacks sing only when many other whales are in the vicinity, it is clear that song is far more common during the feeding season than previously thought. Similar results indicating relatively high levels of balaenopterid singing during the feeding season are emerging from studies on blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales (Croll *et al.* 2002; Moore *et al.* 2002; Clark & Gagnon 2004). This raises the question of why males (in this case male humpback whales) sing so frequently at a time of year that is outside the winter breeding season, and in a location where the principal activity is foraging.

In his review of the social ecology of humpback whales, Clapham (1996) discussed the observations of Mattila *et al.* (1987) and McSweeney *et al.* (1989) and suggested that singing in high latitudes during summer represents low-cost advertisement by males as well as a possible means of assessment by females of males. Clapham linked feeding-ground songs to the high rates of association between males and females in summer (Clapham 1993), and suggested that this reflected a reproductive strategy in which males established bonds with many females during the feeding season with a possible payoff on the breeding grounds in winter. In this hypothesis, any male reproductive success gained from singing in high latitudes is deferred until the winter breeding season.

An alternative hypothesis is that singing on a feeding ground is an attempt to secure immediate matings with sexually mature females who failed to conceive during the previous winter. Data from commercial whaling catches and observations of living animals indicate that most

humpback whale calves are conceived and born in winter. In the Northern Hemisphere, most calving occurs between December and April, with a peak in February (Nishiwaki 1959; Herman & Antinoja 1977; Whitehead 1981). Matings outside this period result in aseasonal conceptions. Given that the gestation period of humpback whales is 11–12 months (Chittleborough 1958), such matings might also result in aseasonal births; however, as there is some overlap between the breeding and feeding seasons, it is possible that a calf conceived in early summer could be born late the following winter in tropical waters.

If aseasonal conceptions occur in humpback whales, these should be manifest in foetal length data obtained from commercial whaling catches. Because of the seasonal nature of humpback whale breeding, foetuses exhibit a non-random distribution characterized by lengths that increase gradually over the course of the year. A foetus resulting from an aseasonal mating in late spring or summer should lie well outside the primary length distribution.

There has been no systematic review of whaling catch data in this regard. However, examination of published datasets on humpback whale foetal lengths reveals several obvious outliers (see Mathews 1937, fig. 53; Chittleborough 1958, table 1; Nishiwaki 1959, fig. 13; and Mikhalev 1997, table 2). Two outliers were also found in unpublished foetal length data ($n = 216$ foetuses) derived from catches of humpback whales off California in the 1920s (see Clapham *et al.* 1997).

These data indicate that aseasonal conceptions, although rare, do occur. Although we do not know where the sexual activity that led to these conceptions took place, the virtual absence of humpback whales from tropical breeding areas in spring and summer leads us to believe that at least some of these matings occurred on the feeding grounds. More significantly, because humpbacks arrive in high latitudes beginning in early spring, it is quite possible that some of the smaller foetuses within the range of the *principal* length distribution were conceived in the feeding areas rather than on the winter breeding grounds.

We do not dispute that most sexual activity in humpback whales occurs in the tropics in winter. Indeed, the number of singers detected in our monitoring area was considerably lower than would be heard in any comparably sized humpback whale low-latitude habitat during much of the winter. However, given the results reported here, we propose that the breeding season should no longer be considered as being strictly confined to lower-latitude regions. We suggest that breeding extends geographically and temporally onto feeding grounds in spring and early summer, and that the frequency of song recorded in the WGB and GSC areas at this time reflects this. Male intrasexual competitive behaviour, occasionally observed on feeding grounds in late autumn (Weinrich 1995), is presumably another manifestation of this phenomenon.

These results underscore the flexibility of mammalian mating systems, and we suggest that singing by male humpback whales in spring and summer represents low-cost opportunistic advertising by males to court females who failed to conceive the previous winter. An alternative hypothesis, that song serves primarily as an intra- (not inter-) sexual display, has been suggested by Darling & Bérubé (2001), who genetically sexed whales that joined singers in Hawaii and found all to be male. However, as has been argued elsewhere (Clapham 2000), this does not necessarily invalidate the female attraction hypothesis because in many taxa males displaying to females frequently attract aggressive approaches from other males. Although observations of female humpback whales approaching singers are rare, they are not unknown (Medrano *et al.* 1994). However, we acknowledge the possibility that singing may function (secondarily or even primarily) to mediate interactions between males.

The timing of the songs relative to the whales' return migration is important. Although there are no data on this timing from our acoustic monitoring area, daily whale-watching-based sampling is conducted in an adjacent area, Massachusetts Bay, between mid-April and October each year (J. Robbins, unpublished data). In 1998, this area was one of the major aggregation sites for Gulf of Maine humpback whales, and their timing of arrival in the region was probably representative of the Gulf of Maine population as a whole. Out of the individually identified whales documented there in that year, 40% had been seen at least once by the end of May, 73% by the end of June and 92% by the end of July. Thus, the evidence suggests that most had completed their northbound migration by June. Because these data are broadly representative of other years, the period in which singing was recorded in 2000 probably included a mixture of newly returning whales and animals that had been on the feeding grounds for some weeks.

If song production is mediated by seasonal elevations in male testosterone levels (as occurs in other taxa; Wingfield & Marler 1988), then spring and autumn singing may represent a residual behaviour that occurs towards the beginning (autumn) or end (spring) of the principal winter mating season (Clapham 2000). This would be consistent with relatively high levels of sperm found in two male humpbacks killed off eastern Canada in October and November (Mitchell 1973). In birds, singing behaviour can be induced in males through testosterone implants, even in the absence of females (Baptista & Morton 1988; Wingfield *et al.* 1990). If song is indeed a hormonally triggered epiphenomenon that occurs in the terminal stages of a migration, it is possible that singing at such times has little reproductive significance. However, the existence of aseasonal conceptions argues against this.

Irrespective of its potential significance to male reproductive success in high latitudes, if singing is driven by elevated testosterone levels we would predict that song would be rare in mid-summer when these levels are depressed. The decline in detections of song towards the end of our study period in June is consistent with this hypothesis. However, additional continuous acoustic monitoring is necessary to determine whether singing indeed continues into the middle of the feeding season, and whether frequent singing is a feature of other humpback whale feeding grounds worldwide.

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